Evolutionary developments in the Silurian Retiolitidae (Graptolites)

Evoluční rozvoj silurských retiolitidních graptolitů

(3 figs)

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Silurian retiolitid graptolites first appeared during the early part of the Aeronian Stage, and underwent considerable diversification in late Aeronian – earliest Telychian, during which time interval more than thirty species were present globally. A lesser, but significant species peak was again reached in the early Homerian (the lundgreni Biozone) prior to the major lundgreni extinction event, as a result of which only one species survived. The last retiolitid became extinct during the leintwardinensis Biozone (mid Ludlow). The two most striking evolutionary changes, important at the subfamily level, involved the change from outward-facing list seams on the ancora sleeve and smooth or linear striations on the list surfaces (seen in most older forms), to inward-facing seams and lists with a pustulose surface (seen in lundgreni Biozone and all younger forms as well as in the older Sokolovograptus). Other generalized trends up the stratigraphic column include: loss of preservation of the sicula; more than a twofold lengthening of the sicula; shallowing and decrease in complexity of the ancora umbrella; reduction of the ancora sleeve; change in thecal profile from early orthograptid to later climacograptid; change from a nema attached to the lists throughout, to a nema either attached only distally, often to an appendix, or being a completely “free” nema; development of an appendix in younger forms, and an internal or external nematulurium only in some “open-ended” forms; development of the upper apertural list in the early Homerian with complex apertural processes in some forms; marked decrease in size from rhabdosome lengths greater than 100 mm in early forms to two to three millimeters in youngest forms, as well as a tendency towards the simplification of the rhabdosome as expressed in the reduction of thecal and ancora sleeve lists, and accompanied by a marked increase in the length of the sicula.

Key words: Silurian, retiolitids, evolution, list seams, ancora, ancora sleeve

Introduction

The Silurian retiolitids, corresponding to the current restricted use of the Family Retiolitidae Lapworth 1873 (see e.g., Melchin 1998), are a group of graptolites “composed of a network of lists of microfuselli and bandaging, developed from the sicula, nema and thecal walls (thecal framework), and by bifurcation of virgella (ancora sleeve)” (Kozłowska-Dawidziuk 1995, p. 1). In the vast majority of cases, retiolitids are preserved only as a network of lists belonging to the theca framework and ancora sleeve. Except for the earliest taxa, the sicula is rarely preserved. In extremely rare cases, however, very thin fusellar thecal periderm, and ancora sleeve periderm infilling all spaces between the lists of ancora sleeve and the thecal periderm, are preserved (Lenz 1994a; Bates – Kirk 1997; Kozłowska-Dawidziuk 1997, and personal observations Kozłowska-Dawidziuk, Lenz – Melchin 2000). This demonstrates that during their life, all retiolitids, at least in more mature stages, were entirely covered with a periderm and had fully developed siculae, making their relationship to “normal” diplograptids self-evident, although the fusellar layer is extremely thin and the main part of skeleton is cortex that makes up most of the lists. Thus the fusellar layer typical for other graptolites is rarely preserved.

Rietiolitids are a complex group, and early efforts at understanding their evolutionary history, using flattened material, have been largely inadequate. The advent of the SEM, and working with isolated, uncompressed ma-
ula and thecal pattern, as well as characters from the previous division of the group, to make a new proposal for the evolutionary history and relationships among the retiolitid lineages.

The present paper is an updating and review of the biostratigraphic ranges, and of the general evolutionary patterns seen the retiolitids, based largely on our recent studies of isolated, uncompressed material from Arctic Canada and north-eastern Poland.

**Biostratigraphic ranges of retiolitids**

In comparison with “normal” graptolites, retiolitids are generally more difficult to recognize or be seen on the rock surfaces when flattened and, when found, they can be difficult to identify with certainty because of their complex morphology. On the other hand, isolated, uncompressed material permits full examination of morphologic complexities, and the specimens can be identified with confidence. Unfortunately, there are relatively few places in the world where long sequences of rocks contain graptolites, including retiolitids, which are preserved in uncompressed form, and can be recovered by acid dissolution of the rocks. Arctic Canada and the Baltic region, including the subsurface of northeastern Poland, stand out as very unique and noteworthy exceptions. In both regions, most of the graptolites are uncompressed and recoverable by acid dissolution providing beautiful preservation as well as a higher diversity than elsewhere and, moreover, these kinds of graptolites range through almost the entire Silurian. As a consequence, the graptolite sequences of these two regions weigh heavily in our assessment of the evolutionary “burst” is impressive. Each of the genera Retiolites, Paraplectograptus, Stomatograptus, and Sokolovograpthus, each of which is marked by very distinct and different morphological characteristics – for example, the first three genera may possess a nematularium and stomata, while Sokolovograpthus lacks both – and each is comprised of several or more species.

The late Aeronian to early Telychian appears, then, to have been a time of considerable retiolitid innovation. Furthermore, when the number of species is factored in, the evolutionary “burst” is impressive. Each of the genera Pseudoretiolites, Pseudoplegmatograptus, Retiolites, Paraplectograptus / Pseudoplegmatograptus, Sokolovograpthus and Stomatograpthus (including Sinostomatograpthus) is represented by three to six species, and “Retiolites”, “Paraplectograptus” and “Rotaretiolites” are each represented by at least one species. The total species diversity in the early part of the Telychian therefore, probably exceeded thirty, coinciding with a similar high diversity of monograptids (e.g., Melchin et al. 1998).

The Sheinwoodian appears to have been relatively quiet, with only Eisenackograptus, the earliest member of the very important Gothograptus group (see Kozłowska-Dawidziuk, 2001), appearing in the upper Sheinwoodian, rigidis-perneri Biozone. The succeeding lundgreni Biozone (lower Homerian) represents a crucial time in retiolitid history. Retiolites, Stomatograptus, Paraplectograptus and Sokolovograpthus become extinct about midway through the biozone (Lenz – Kozłowska-Dawidziuk, 2001) as shown in Poland and Arctic Canada. Eisenackograptus ranges only to the top of the biozone prior to its extinction during the “lundgreni extinction event” (Koren 1991).

The lundgreni Biozone is uniquely marked by the appearance and proliferation of a new element, Cometograptus, of which there are six species in Arctic Canada, and two different species in north-eastern Poland.
(Kozłowska-Dawidziuk 2001; Lenz – Kozłowska-Dawidziuk 2002a), all of which become extinct at the end of the biozone. Finally, and most importantly, the lundgreni Biozone witnesses the appearance of Gothograptus, the only retiolitid taxon to survive the extinction event (Kozłowska-Dawidziuk 1990) and which was, probably, ancestral to all subsequent retiolitids. Gothograptus ranges to at least the late Homerian praedeubeli-deubeli Biozone (Kozłowska-Dawidziuk et al. 2001). The immediate post-extinction interval, the nassa-dubius Biozone, is relatively quiet with only the numerous Gothograptus nassa, and a few geographically restricted occurrences of Spinograptus in the upper part of the biozone (see Kozłowska-Dawidziuk et al. 2001).

Several new genera with nematularia appeared during the praedeubeli-deubeli Biozone, and ranged to the top of the Homerian (described by Lenz – Kozłowska-Dawidziuk 2002a). Spinograptus, some forms of which possessed an appendix, became common and widespread at this time and ranged into the lower part of the Lower Ludlow; during this time-range interval it proliferated into five species: S. clathrospinosus, S. latespinosus, S. lawsoni, S. reticulolawsoni, and S. spinosus. In the upper half of the upper Homerian, therefore, nine to ten species of retiolitids existed globally (see Lenz – Kozłowska-Dawidziuk et al. 2002b). Plectograptus appears at this time too, but is rare and apparently geographically restricted.

The Lower Ludlow witnessed the continuation of Spinograptus, the widespread distribution and modest proliferation of Plectograptus as well as further derivatives such as Semiplectograptus and Plectodinemagraptus. The latter two are the youngest known retiolitids, found so far only in northeastern Poland (Kozłowska-Dawidziuk 1995). There is also continuation and diversification of the Gothograptus lineage as represented by Neogothograptus and later Holoretiolites. Species diversity reached at least seven or eight during the upper Gornian, not long before the total extinction of the retiolitids.

The Ludlow witnessed two patterns of rhabdosome development: rhabdosomes that were relatively large and “open-ended” (e.g., Plectograptus and at least some Spinograptus, both of which sometimes developed nematularia), and those that were relatively small and possessed an appendix (e.g., Neogothograptus and Holoretiolites). A more or less equal number of species in each subgroup existed during this time. There is, however, very little information on whether one subgroup preceded the other in its disappearance, or whether the two subgroups were extinguished more or less simultaneously. At the moment, Plectodinemagraptus, a plectograptid, appears to represent the last surviving retiolitid.

Fig. 1 Biostratigraphic ranges of retiolitid genera, showing position of ancora sleeve list seams, long siculae, and pustulose bandages on lists.
Evolutionary trends in the Retiolitidae

Retiolitid ancestry

There is general agreement that the ancestry of the Silurian retiolitids lays with some Pattern I ancorate petalolithid such as Petaloilithus or Pseudorthograptus (Rickards et al. 1977; Mitchell 1987; Bates – Kirk 1992; Kozłowska-Dawidziuk 1995; Lenz – Melchin 1997; Melchin 1999). The rare occurrence of retiolitids possessing a complete periderm (see Lenz 1994a), and the discovery of a form that immediately pre-dates the earliest retiolitid and possesses characteristics more or less intermediate between the petalolithids and retiolitids (Melchin 1999), adds further strong support to this interpretation. The development of the retiolitids is then perceived to unfold in the following manner, although the actual steps are obscure: beginning with some “normal” petalolithid with a normally-developed periderm and well-developed ancora, the next step was the increasingly distal development of the ancoral lists to the point where they essentially entirely enveloped the thecae. Ventrally and distally, one opposing pair of primary ancora lists divided and lengthened, and were incorporated into the thecal rims and lips, and generally in the lateral parts of the rhabdosome, comprising the thecal framework (Bates 1990). The other pair of opposing primary ancora lists divided and lengthened frequently, but in a less precise way to form a separate layer over the lateral walls. This layer, the ancora sleeve of Bates (1990), lies outside and is separate from the thecal framework list layer, but is ventrally attached to the thecal framework (see Lenz 1994a; Kozłowska-Dawidziuk 1997, Lenz – Thorsteinsson 1997). The ancora sleeve is a unique structure, being known only among the retiolitids, and its relationship to the thecae is not fully understood.

List structure and micro ornamentation

Lists are built of microfuselli and bandages that, layer-by-layer, increase in thickness as the rhabdosome matures (Bates 1987). As a result, ancora sleeve lists and thecal lists all possess seams along their lengths. These seams occasionally retain poorly preserved shard-like incremental remnants of the once-continuous fusellar layer (Bates 1987).

List micro ornamentation, in the form of a smooth surface or parallel striations, is characteristically found on the lists of most older retiolitids, including Pseudoretioilites, Pseudoplegmatograptus, Stomatograptus, Retiolites, “Rotaretiolites”, “Paraplectograptus” and Rotaretiolites. In all of these taxa, the seams of the ancora sleeve are situated on the outside, suggesting that list secretion proceeded from the inside. Beginning with Paraplectograptus and Sokolovograptus, new micro ornamentation developed in the form of pustules, while ancora sleeve list seams face out and in, respectively. All subsequently appearing retiolitids are more or less pustulose. Eisenack-ograptus appears in the upper Sheinwoodian, and its lists are entirely pustulose; however, while possessing mostly outward facing list seams (in-facing ornamentation), some ancora sleeve list seams are in-facing. Cometograptus, confined to the Lundgreni Biozone, is the youngest appearing form with mostly outward-facing list seams of the ancora sleeve, but its ornamentation is entirely of weak to strong pustules (Kozłowska-Dawidziuk 2001, Lenz – Kozłowska-Dawidziuk 2002a). The lists of all remaining, younger retiolitids bear pustules and in-facing list seams. Sokolovograptus (Figs 3.18, 3.20) is, however, an anomaly in appearing so early (Fig. 1), but in possessing the “advanced” characteristics of inward facing list seams and external pustulose ornamentation. It was possibly ancestral to some of the post-extinction retiolitids, although there is no form that appears to be directly related to Sokolovograptus and it may, instead, have been an early, but isolated offshoot.

Sicula preservation

It is clear that retiolitids possessed a fully functional sicula during their lifetime. The retiolitid sicula was, however, a very delicate structure, and was commonly partially preserved only in the earlier retiolitids. The prosicula and part of the metasicula is commonly preserved in Pseudoretioilites (Figs 2.6, 2.9), while only the prosicula is preserved in Pseudoplegmatograptus, “Rotaretiolites” and “Paraplectograptus” (see Lenz – Melchin 1997). In Stomatograptus (Figs 2.10, 2.11) the prosicula is most often preserved, while in Retiolites and Paraplectograptus it is rarely preserved in full (Kühne 1953; Obut – Zaslavskaya 1976, Kozłowska-Dawidziuk 1995; Bates – Kirk 1997), but may be represented by a thickening or sicula threads (Lenz – Melchin 1987a). Rotaretiolites (Fig. 3.11) does not preserve the prosicula, but often retains a complete prosicular ring (Bates – Kirk 1992) and sometimes, a prosicular longitudinal list. A prosicula has been observed in Sokolovograptus (Obut – Zaslavskaya 1976), but is an extremely rare occurrence.

Younger retiolitids only occasionally retain fragments of the prosicula ring and/or of a longitudinal list; however, prominent sicular seams visible along the virgella (virga), permit recognition of the position and length of both the prosicula and metasicula (Bates – Kirk 1997, Kozłowska-Dawidziuk 1998). In extremely rare cases where the rhabdosome retains a complete periderm, the sicula is also fully preserved (Lenz 1994a, Kozłowska-Dawidziuk 1997).

Sicula development

Bates – Kirk (1992) and Kozłowska-Dawidziuk (1998) recognized the differing lengths of siculae present in the different groups of retiolitids. Bates – Kirk (1992) recognised two basic size classes, while Kozłowska-Dawidziuk (1998) has recognized three. All but one of the oldest taxa (Pseudoretioilites, Pseudoplegmatograptus,
Rotaretiolites, Retiolites, Stomatograptus, and “Paraplectograptus” have short siculae (< 1.0 mm). The Paraplectograptus (including Pseudoplectograptus) group whose age-range overlaps entirely with Retiolites and Stomatograptus, and Gothograptus, have slightly longer siculae (about 1.4 mm). Eisenackograptus, appearing in the upper Sheinwoodian, Cometograptus, confined to the lower Homenian, and all the youngest forms (Spinograptus, Neogothograptus, Plectograptus, and Holoretiolites) have long siculae (2.0–2.5 mm). Sokolovograptus, while entirely overlapping in age-range with Retiolites and Paraplectograptus, also possesses a very long sicula.

The fact that Sokolovograptus appears so early yet has a long sicula, and inward facing list seams (i.e., “advanced” characteristics), makes it anomalous.

The presence of varying sicula lengths in different taxa has prompted the proposal of a polyphylectic/diphylectic origin of the retiolitids (Bates – Kirk 1992). However, since sicular lengths in general increase up the stratigraphic column, that interpretation is unlikely, or at least, unnecessary.

Ancora development

The ancora umbrella of the earliest retiolitids, like that of some of their purported ancora-bearing petalolithid ancestors, was deep and bowl-shaped (as in Pseudoretio-
lites, Fig. 2.6), and bore a double spiral thread (Bates – Kirk 1984), as did “Rotaretiolites” and “Paraplect古城graptus” of Lenz – Melchin (1997). The slightly younger taxon Rotaretiolites possessed a simple, shallow ancora umbrella composed of four-pronged ancora lists with single horizontal lists along the rim (Fig. 3.11), but still retained the spiral list structures.

Ancora umbrellas of Pseudoplectograptus, Retiolites (Figs 2.2, 2.5) and Stomatograptus (Figs 2.10, 2.11) were shallow, but the primary ancora lists further subdivided distally, resulting in a somewhat more complex polygonal pattern, and more complex rims. Pseudoplectograptus still retained the double-spiralled threads. Ancora umbrellas of subsequent taxa were relatively shallow and simple: in Paraplectograptus and Sokolovograptus, the ancora lists bifurcate, but the umbrella is simple and extremely shallow (Fig. 3.20); in a second group such as Eisenackograptus, Gothograptus and Spinograptus, the ancora lists bifurcate and the distal margin of the umbrella possesses somewhat more complex list structures along the rim; and in the youngest group, Plectograptus, Semi-plectograptus and Plectodinemaplectograptus, the umbrella is extremely simple and shallow, and two of the four primary ancora lists that make up the four meshes are usually under-developed (Figs 3.4, 3.9, 3.21).

Ancora sleeve

The ancora sleeve, which is present in almost every reti-
olitid, is the next stage of development from the ancora umbrella and begins as lists connecting with the first th-
ecae. The first known retiolitids such as the Pseudoretio-
lites, Pseudoplectograptus, Retiolites and Stomatograptus groups possess well-developed ancora sleeves in which the list seams face outwards. The structure is built as a network of thin lists referred to as reticulum. The reticular lists are connected with stronger internal lists belonging to the thecal framework. The maximum of complication of the ancora sleeve development is reached in Pseudoplectograptus, where it is developed as two layers: an inner layer with seams on lists facing outwards, and the outer layer with seams on lists facing inwards (Bates – Kirk 1992, 1997). Thus there is a space between the thecal wall and ancora sleeve, as well as a space between two ancora sleeve layers in the rh-
dosome. Other older forms such as Paraplectograptus and Pseudoplectograptus (Figs 2.1, 3.15), often possess much simpler ancora sleeves. A similar model of that structure, composed of thin, mostly irregular lists, occurs in Sokolovograptus. In that lineage, some trend towards the thick-
ening and horizontal arrangement of the lists in distal parts of the rhambosome is observed; furthermore, there is a ten-
dency towards a strong reduction of lists to the point where relatively few lists remain (Kozłowska-Dawidziuk 2001). The difference between Sokolovograptus and oth-
er older, but coeval forms, is that its list seams face in-
wards. Rotaretiolites is an exception among older forms, in not having developed an ancora sleeve (3.31).

Among species of the Cometograptus group, confined to the landgren Biozone, there is a range of variation in the development of the ancora sleeve from many irregular thin lists as in Cometograptus apo-
xis, to the regular thick lists in C. tomczyki (Lenz 1993; Kozłowska-Dawidziuk 2001) (Figs 2.13, 3.8). The most spectacular re-
duction of the ancora sleeve is, however, observed in the Gothograptus lineage. In its first representative, Eisen-
ackograptus (Fig. 3.5), the ancora sleeve is built of a dense network of irregular thin lists with list seams fac-
ing outwards, while on some thicker lists the list seams face inwards. In succeeding forms such as Gothograp-
tus, Neogothograptus and Holoretiolites, the list seams of the ancora sleeve all face inwards, and they exhibit a ten-
dency towards reduction in the number of thin lists, as well as a further reduction in the number of thicker lists, the so-called clathrium (Figs 3.2, 3.4, 3.17). A similar trend in the reduction of reticular and clathrial lists is observed in the Spinograptus and Plectograptus lineages, until in the final member – Plectodinemaplectograptus gracilis – there appears to be no ancora sleeve (Figs 3.7, 3.9).

The trend in the reduction of the ancora sleeve up the stratigraphic column is accompanied by a concomitant decrease in the size of entire colony, as well as in the number of thecae. However, the structural development between thecal wall and ancora sleeve wall is still not un-
derstood in many forms, particularly in those in which the seams lists face in, although Bates – Kirk (1992, 1997) have made preliminary studies of some of the older forms. As a result, evolutionary trends in many forms are not well understood.
Thecal profile

As already noted, retiolitid thecae were made of extremely thin fuselli and for this reason are normally not preserved; as a result, it is only rarely that the actual thecal walls are observable. Recognition of the thecal profile is possible, however, using traces such as transverse rods and thecal lip position, as well as ventral margin of the thecae preserved as lists such as mid-ventral, sigmoidal or inner connecting lists. Exceptionally, some or all of the thecal periderm is preserved (Lenz 1994a; Lenz – Thorsteinsson 1997), making thecal profile unequivocal. The thecae of most of the oldest taxa – Pseudoretiolites, Rotaretiolites, Pseudoplectograptus, Retioites and Stomatograptus – were clearly orthograptid in profile (Figs 2.2, 2.4, 2.6, 3.16). This is demonstrated by the presence of mid-ventral thecal list in taxa such as Pseudoretiolites and Rotaretiolites, and by the rare preservation of thecal ventral walls in Retioites and Stomatograptus (Holm, 1890; Lenz – Melchin, 1987b; Lenz – Thorsteinsson, 1997). Paraplectograptus and Pseudoplectograptus probably also exhibited orthograptid thecal profiles (Figs 2.1, 3.15), as shown by the inclined genicular wall posterior of the apertural lip and position of transverse rods in Pseudoplectograptus sagenus (Lenz 1993). The thecal profile in Sokolovograptus is not clear, but could have been either glyptograptid or climacograptid (Fig. 3.20).

The orthograptid thecal profile disappeared together with the oldest groups of retiolitids during lundgreni Event. This was replaced by a climacograptid profile, beginning in the early Hermonian (earlier if Sokolovograptus possessed a climacograptid profile) with the appearance of the lundgreni Biozone forms Gothograptus and Cometograptus, and continued in all post-extinction retiolitids. The presence of a complete periderm on “Agastograptus robustus” Obut – Zaslavskaya” described in Lenz (1994a), and on Spinograptus (Kozłowska-Dawidziuk 1997) (Fig. 2.3) convincingly demonstrates this. Only Eisenackograptus (Fig. 3.5) is unusual in that it clearly possesses thecae with a pseudoglyptograptid profile (Lenz 1994a). Generally speaking, a long sicula and pustular ornamentation accompanied the climacograptid-profile retiolitids. Thecal profile is a feature that confirms the Pattern I (Pattern R of Melchin 1998) astogenetic development of retiolitids.

Virgula/Nema attachment

Internally, the virgula/nema of all older retiolitids from Pseudoretiolites to Stomatograptus (see Fig. 1) was an integral part of the rhabdosomal framework in being directly joined to the thecal framework (Figs 2.1, 2.2, 2.10). In Sokolovograptus, and in Cometograptus, Spinograptus and Plectograptus, and the youngest genera of the Gothograptus lineage (Neogothograptus and Holoretioites), as well as in new post-lundgreni genera (Lenz – Kozłowska-Dawidziuk 2002b?), the virgula/nema appears to be unattached, or only loosely attached to the distal-most parts of the open-ended rhabdosome distal of the ancora (Figs 3.2, 3.4, 3.20, 3.21).

It is interesting to note the trend to loose contact of the nema with the rhabdosomal framework through the Gothograptus lineage, the first lineage with a developed appendix. The pre-lundgreni forms of this lineage possess a nema fused to the lateral wall of the ancora sleeve, whereas in post-extinction representatives of the lineage, represented by Neogothograptus and Holoretioites, the nema has a central position in rhabdosome as it has in every other retiolitid of this interval. The overall trend is thus toward a length-increase in the sicula, and larger central common canal, suggesting a different organisation of the colony.

Appendix and nematulianum

A nematulianum, as a spiral structure, a one-vane thickening or a three-vane structure, was fairly common among the petalolithids (e.g., see Hundt, 1965; Lenz, 1982). The spiralled nematulianum, or a much-thickened nema, was also occasionally present in retiolitids (see...
e.g., Kozłowska-Dawidziuk et al. 2001). Although the thickened structure was generally present outside the body of the rhabdosome (Fig. 2.12), it sometimes developed internally (Lenz – Melchin 1987a; Kozłowska-Dawidziuk et al. 2001, Lenz – Kozłowska-Dawidziuk 2002a).

A nematarium has been observed in some older retiolitids such as “Pseudoplegmatograptus” (Storch 1992), Stomatograptus, Paraplectograptus and Pseudoplectograptus (Figs 2.7, 2.8, 3.15, 3.19) as well as in the younger (lower Homerian, lundgreni Biozone) forms. Other older “open-ended” retiolitids (i.e., those without an appendix) probably also possessed nemataria that have not been preserved. Similar nemataria have recently been observed in new genera from post-lundgreni interval (Lenz – Kozłowska-Dawidziuk 2002a) and in the Ludlow, as in Plectograptus macilentus (Bouček – Münch 1952). Nematarium could have been related to orientation and vertical movement in the water column.

A different way of life is suggested by those retiolitids with an appendix at the end of the rhabdosome. The first forms with an appendix, the members of the Gothograptus lineage, appear in the late Sheinwoodian (Eisenackograptus), but proliferate in the lundgreni Biozone beginning with the appearance of the oldest Gothograptus. In the older members of the lineage (Eisenackograptus and Gothograptus) (Figs 3.4, 3.5), the appendix can be as long as the thecal part of the rhabdosome, whereas in the younger (Ludlow) forms such as Neogothograptus and Holoretiolites, it was normally very short to almost rudimentary, although occasionally in some forms it can be long (Fig. 3.4). An appendix is also sometimes present in some Spinograptus (see Lenz, 1994a; Kozłowska-Dawidziuk, 1997).

Apertural processes

The evolution of apertures in retiolitids occurs in two stages. The oldest types lacked upper apertural lists and in only a few taxa such as Pseudoplegmatograptus and “Rotaretiolites”, simple paired spines were present along the lateral margins of the thecal aperture lists. More complex apertural structures in the form of “thecal hoods” were developed in the first two or three thecal pairs of some specimens of Retiolites (Fig. 2.2). Since, however, specimens with and those without thecal hoods occur in the same collections and are otherwise identical, the presence of a thecal hood is considered to be intraspecific variation.

Spines and genicular processes – some very complex – become much more common in younger forms, beginning in the early Homerian, and occur in some species of Cometograptus [e.g., C. tomczyki (Fig. 3.8), C. koreni, and C. nevadensis] (see Kozłowska-Dawidziuk 2001). These processes are particularly prominent in C. apoxyx (Fig. 2.13) in which the supra-apertural genicular processes are complex, well developed, and connected to the ancora sleeve (Lenz – Kozłowska-Dawidziuk 2002b?).

An important new morphological development, the upper apertural list, first appeared within the Gothograptus group in the lower Homerian, lundgreni Biozone. The appearance of the upper apertural list and accompanying lateral thecal lists permitted the development of a rounded or oval thecal aperture and an array of different kinds of apertural processes. In G. kozłowski, for example, proximal thecae possessed microfusellar hoods, medial thecae bore spines and loops, and distal thecae developed reticular hoods (Figs 3.3, 3.12), whereas in
G. obtectus and G. nassa (Figs. 3.1, 3.13), large thecal hoods were present throughout and often completely hid the thecal apertures. In post-_lundgreni_, upper Homerian retiolitids, apertural processes are common, especially in _Spinograptus_ group (S. spinosus, S. clathrospinus, S. latespinosus, S. munchi), in which complex, paired reticulofusellar processes of greatly varying length, width and complexity were developed on the upper apertural list (Fig. 3.10). Single complex, lacy reticular hoods also appeared in other taxa at this time (Lenz 1994a; Lenz ñ Kozłowska-Dawidziuk pers. observation 2000). The youngest members of the _Gothograptus_ group, _Neogothograptus eisenacki_, appearing in earliest Ludlow, possesses up to 19 pairs of thecae; simultaneously, however, some populations include forms possessing as few as 19 pairs of thecae and are without any kind of apertural process (Figs. 3.7, 3.9).

It appears then, that the appearance complex apertural structures/genicular processes coincided with the development of the upper apertural list, a structure that appeared only in the early Homerian. By comparison, the _Sokolovograptus_ and _Paraplectograptus_ lineages that range into the early Homerian, lack upper apertural lists and are without apertural processes.

**Stomata**

Stomata along the lateral wall of the ancora sleeve are relatively common in the earlier retiolitids, being found in _Pseudoretiolites, Pseudoplegmatograptus_ and, especially _Stomatograptus_ (Figs. 2.7, 2.8). The structure appears to have arisen again, possibly independently, in the early Homerian where it is found only in some species of _Cometograptus_ (e.g., _C. apoxys_) (see Lenz 1993). Stomata are only rarely known beyond the post-_lundgreni_ extinction event, as in the case of one specimen of _Spinograptus_ sp. with preserved membranes (Fig. 2.3).

**Ancora sleeve spines**

These novel structures have been recently described as seamed spines present on the ancora sleeve of _Cometograptus_ (Kozłowska-Dawidziuk 2001). The spines are located along the central part of the lateral wall of the ancora sleeve, and have outward-facing seams that are a continuation of the ancora sleeve list seams (Fig. 3.8).

**Size**

As already noted by Lenz – Melchin (1997), the retiolitids, in general, show an overall steady trend toward size reduction up the stratigraphic column. Taxa such as _Reticulites, Pseudoplegmatograptus_, and _Stomatograptus_ sometimes exceeded 100 mm in length and 8–10 mm in width (see e.g., Bouček – Münch 1943; Lenz 1982); “mid-range” taxa such as _Sokolovograptus_, _Spinograptus_, _Gothograptus_ and _Paraplectograptus_ may attain 10–15 mm in length and two to three mm in width (Fig. 3.1); and “end-members” such as _Neogothograptus_ and _Holoretiolites_ are generally no more than 2 mm to 5 mm long and about one mm wide (Figs. 3.2, 3.4, 3.16, 3.17).

The size trend is further illustrated in two examples. The _Gothograptus_ lineage first appears in the early Homerian and continues to the almost the highest range of the retiolitids. The early Homerian representative, _Eisenackograptus eisenacki_, as well as _G. nassa_, appearing in the earliest late Homerian, may possess as many as 19 pairs of thecae; simultaneously, however, some populations include forms possessing as few as three thecal pairs (Fig. 3.5). A younger member of that lineage, _Neogothograptus_, appearing in earliest Ludlow, possesses up to seven pairs of thecae and often fewer (Figs. 3.16, 3.17); whereas the slightly younger _Holoretiolites mancki_ may possess no more than two thecal pairs.

The _Plectograptus_ lineage is further illustrated. The lower Ludlow forms, _P. macilentus_ (Fig. 3.21) and _P. wimani_ attained rhambods with widths of about 2.5 mm; the succeeding _Semiplectograptus_ attains about 1.7 mm in width; and the youngest member, _Plectodinemagraptus_ is only about 0.7 mm wide. In all of the above reductions in size, there is a concomitant reduction first in reticular lists, followed by a reduction in ancora sleeve lists, which seems almost completely reduced in the last representative, _Plectodinemagraptus gracilis_ (Figs. 3.7, 3.9).

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Evoluční rozvoj silurských retiolitidních graptolitů

Retiolitidní graptolit se v siluru objevují poprvé ve starší ortograptidním otoku a výšších biotopenách těžce procházejících pozoruhodnou diverzifikací. V tomto časovém úseku se tak objevuje více než třetina druhů. Méně významný vrchol druhového rozvoje přichází ve spodním wostenianu (biozóna lungreni) a předchází významnějšímu vymizení v průběhu této biozóny, jehož důsledkem bylo přežití jediného druhu. Poslední retiolitum vymizává v průběhu biozóny leintwardinensis ve středním ludlowu. Na úrovni podřádu jsou významnějšími vývojovými změnami: přechod od dovnitřní obrácených ovoce na lištové nástavce kotvící a podélní střiace nebo hladké povrch lišt (viditelné na většině taxonů) k dovnitřní obráceným ovoce se vyslovením profilu těky od časně ortograptidního typu k pozdějším climacograptidním taxonům. Dalšími trendy jsou změny od dobře zpevněných silikátorů ke kotvící a podstatně zjednodušení kotvící; redukce nástavce kotvící; změna profilu těky od časně ortograptidního typu k pozdějším climacograptidnímu taxonům; Dalšími trendy jsou změny od dobře zpevněných silikátorů ke kotvící a podstatně zjednodušení kotvící; redukce nástavce kotvící; změna profilu těky od časně ortograptidního typu k pozdějším climacograptidnímu taxonům; dalšími trendy jsou změny od dobře zpevněných silikátorů ke kotvící a podstatně zjednodušení kotvící; redukce nástavce kotvící; změna profilu těky od časně ortograptidního typu k pozdějším climacograptidnímu taxonům; dalšími trendy jsou změny od dobře zpevněných silikátorů ke kotvící a podstatně zjednodušení kotvící; redukce nástavce kotvící; změna profilu těky od časně ortograptidního typu k pozdějším climacograptidnímu taxonům; dalšími trendy jsou změny od dobře zpevněných silikátorů ke kotvící a podstatně zjednodušení kotvící; redukce nástavce kotvící; změna profilu těky od časně ortograptidního typu k pozdějším climacograptidnímu taxonům; dalšími trendy jsou změny od dobře zpevněných silikátorů ke kotvící a podstatně zjednodušení kotvící; redukce nástavce kotvící; změna profilu těky od časně ortograptidního typu k pozdějším climacograptidnímu taxonům; dalšími trendy jsou změny od dobře zpevněných silikátorů ke kotvící a podstatně zjednodušení kotvící; redukce nástavce kotvící; změna profilu těky od časně ortograptidního typu k pozdějším climacograptidnímu taxonům; dalšími trendy jsou změny od dobře zpevněných silikátorů ke kotvící a podstatně zjednodušení kotvící; redukce nástavce kotvící; změna profilu těky od časně ortograptidního typu k pozdějším climacograptidnímu taxonům; dalšími trendy jsou změny od dobře zpevněných silikátorů ke kotvící a podstatně zjednodušení kotvící; redukce nástavce kotvící; změna profilu těky od časně ortograptidního typu k pozdějším climacograptidnímu taxonům; dalšími trendy jsou změny od dobře zpevněných silikátorů ke kotvící a podstatně zjednodušení kotvící; redukce nástavce kotvící; změna profilu těky od časně ortograptidního typu k pozdějším climacograptidnímu taxonům; dalšími trendy jsou změny od dobře zpevněných silikátorů ke kotvící a podstatně zjednodušení kotvící; redukce nástavce kotvící; změna profilu těky od časně ortograptidního typu k pozdějším climacograptidnímu taxonům; dalšími trendy jsou změny od dobře zpevněných silikátorů ke kotvící a podstatně zjednodušení kotvící; redukce nástavce kotvící; změna profilu těky od časně ortograptidního typu k pozdějším climacograptidnímu taxonům; dalšími trendy jsou změny od dobře zpevněných silikátorů ke kotvící a podstatně zjednodušení kotvící; redukce nástavce kotvící; změna profilu těky od časně ortograptidního typu k pozdějším climacograptidnímu taxonům; dalšími trendy jsou změny od dobře zpevněných silikátorů ke kotvící a podstatně zjednodušení kotvící; redukce nástavce kotvící; změna profilu těky od časně ortograptidního typu k pozdějším climacograptidnímu taxonům; dalšími trendy jsou změny od dobře zpevněných silikátorů ke kotvící a podstatně zjednodušení kotvící; redukce nástavce kotvící; změna profilu těky od časně ortograptidního typu k pozdější